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Motility of Electric Cable Bacteria

Jesper Tataru Bjerg,[a,b] Lars Riis Damgaard,[b] Simon Agner Holm,[b] Andreas Schramm,[a,b] Lars Peter Nielsen[a,b]

Center for Geomicrobiology, Department of Bioscience, Aarhus University, Aarhus, Denmark[a]; Section for Microbiology, Department of Bioscience, Aarhus University, Aarhus, Denmark[b]

ABSTRACT

Cable bacteria are filamentous bacteria that electrically couple sulfide oxidation and oxygen reduction at centimeter distances, and observations in sediment environments have suggested that they are motile. By time-lapse microscopy, we found that cable bacteria used gliding motility on surfaces with a highly variable speed of 0.5 ± 0.3 μm s^{-1} (mean ± standard deviation) and time between reversals of 155 ± 108 s. They frequently moved forward in loops, and formation of twisted loops revealed helical rotation of the filaments. Cable bacteria responded to chemical gradients in their environment, and around the oxic-anoxic interface, they curled and piled up, with straight parts connecting back to the source of sulfide. Thus, it appears that motility serves the cable bacteria in establishing and keeping optimal connections between their distant electron donor and acceptors in a dynamic sediment environment.

IMPORTANCE

This study reports on the motility of cable bacteria, capable of transmitting electrons over centimeter distances. It gives us a new insight into their behavior in sediments and explains previously puzzling findings. Cable bacteria greatly influence their environment, and this article adds significantly to the body of knowledge about this organism.

Cable bacteria are filamentous bacteria that transport electrons over centimeter distances, connecting spatially separated electron donors and acceptors (1). Strings running longitudinally along the cable bacteria in a periplasmic continuum are thought to conduct the electrons (1). In sediments the electrically coupled sulfide oxidation and oxygen reduction result in a spatial separation between oxygen and detectable sulfide in the pore water and a pH peak in the oxic zone due to cathodic proton consumption (2). Directly and indirectly, the cable bacteria profoundly affect the geochemistry of their sediment environment (3, 4). All cable bacteria found so far have been shown, by single-filament sequencing of 16S rRNA or fluorescence *in situ* hybridization (FISH), to belong to the *Desulfobulbaceae* family, where no other filamentous form is known. Cable bacteria or pore water profiles indicating their presence have been reported from many different places in the world, including a salt marsh (5, 6), a seasonally hypoxic basin (7), a freshwater stream (8), and a subtidal coastal mud plain (7), generally characterized by moderate to high sulfide generation and restricted bioturbation.

Cable bacterium succession in incubations of homogenized sediment exposed to oxygen has a general pattern of fast growth to a peak population density followed by a decline (9, 10). The depth distribution of cable bacteria matches the increasing separation between oxygen and pore water sulfide, and FISH and DAPI (4′,6-diamidino-2-phenylindole) staining show chromosomes in division or separation stages throughout the cable bacteria, suggesting that cells other than just apical cells are actively dividing and have to be moved actively to extend the filaments downwards (9). Additional indication of motility comes from a study of cable bacterium activity underneath a photosynthetic algal mat in an intertidal salt marsh (6). When incubated in an alternating light-dark regime, the sulfide concentration at depth increases rapidly with the transition from light to dark, as oxygen penetration declines when photosynthesis ceases (6). In the hours after darkening, sulfide concentrations at depth decrease again, suggesting that the cable bacteria recovered the lost cathodic activity, likely by moving more cells up into the oxic zone.

In the present study, we systematically investigated cable bacterium motility in designed slide setups using time-lapse microscopy and video analysis. We measured speed and reversal frequency, tested identity using FISH, and observed behavior on time scales up to days.

MATERIALS AND METHODS

Sediment incubations and microscope slide preparations. No pure cultures of cable bacteria are available yet; therefore, enrichment cultures were set up from the same source and with the same treatment as in previous studies (1, 9). Such enrichments are full of sediment microbes, but the very long, filamentous cable bacteria are clearly distinguishable, and other bacteria aid by demarcating the boundary between oxic and anoxic conditions. Sediment was sampled from Aarhus Harbor (56.1388 N, 10.2140 E; water depth, 4 m) with a Kajak sampler (KC Denmark A/S, Silkeborg, Denmark). The top 10 cm of sediment was discarded, and the remaining sediment was sifted through a 0.5-mm-pore sieve to eliminate mesofauna (9). This sediment was then incubated in plastic containers at 15°C in a 10-cm-deep layer with humid air above. To test whether the variation in speed could be attributed to width of filaments or other effects of incubation duration, a time series experiment was set up where a sediment incubation was sampled after 7, 10, 14, 17, 20, 23, and 27 days of incubation.

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Address correspondence to Jesper Tataru Bjerg, jjbjerg@bios.au.dk.

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To observe motility, three types of microscope slide incubations (types A, B, and C) were optimized for rapid high-resolution observations, ease of FISH identification and control of chemical gradients, and long-term observations, respectively. All three types of slides offered an environment with an influx of oxygen from the edge of the slide and diffusion of sulfide from the sediment, creating a gradient environment much like the one that the cable bacteria encounter in natural sediment, with the very notable absence of sediment particles that would otherwise have interfered with observation.

For type A slides, small clumps of sediment were placed on a 26- by 76-mm microscopic slide and squeezed flat with a 25- by 60-mm cover glass. The distance between the microscope slide and cover glass was 100 to 200 μm (see Fig. S1A in the supplemental material). The clumps of sediment were placed in the center of the slide, being close (~1 mm) to the long edge and far (up to 15 mm) from the short edge, creating different levels of exposure to oxygen. The gap between the slide and cover glass was then gently flooded with Red Sea salt artificial seawater, flushing away loose particles of sediment and leaving distinct sediment edges and clear glass surfaces. Any excess water was removed using filter paper, and the slide was sealed with nail polish to limit evaporation but allow diffusion of oxygen into the slide. To create conditions with a more stable oxygen front, type B slides (see Fig. S1B) were constructed by gluing slabs of microscope slide glass onto a microscope slide, creating a chamber in the center of the slide with dimensions 30 mm by 8 mm by 1 mm. Sediment was then placed in this chamber with a cover glass on top, and the narrow gap between the slide and cover glass was flooded with Red Sea salt artificial seawater to remove loose sediment particles. This created a sharp division between the sediment and clear glass, and bacteria could move into the space left between the chamber and edge of the cover glass.

To observe growth and movement of cables, type C slides were constructed from 26- by 76-mm microscope slides (see Fig. S1C in the supplemental material). Two holes were drilled into the slides 1 to 2 cm apart, which were covered with two plastic cylinders glued to the microscope slide with UV curing glue (Loctite 190672; Loctite Corp.) to serve as nutrient reservoirs. On the opposite side of the cylinders, a 10-μm-deep channel was etched between the holes using hydrofluoric acid. One cylinder reservoir was filled with mud containing cable bacteria and closed with a rubber stopper. The other cylinder was filled with water covered with a thin film of paraffin oil to allow oxygen diffusion without excessive evaporation. The small etched channel was covered with a 25- by 60-mm cover glass fixed to the microscope slide with UV curing glue.

Time-lapse microscopy and imaging. Slide preparations were investigated in a phase-contrast microscope at 20°C. A Zeiss Observer Z1 (Zeiss, Göttingen, Germany) inverted microscope with a PALM automated stage using a 40× phase-contrast objective was used for time-lapse micrographs. The microscope scaling and length measurements were calculated using calibrations of the microscope software (Zen Blue Edition; Zeiss, Göttingen, Germany). Large multi-image micrographs were recorded using the automated tiles option in the ZEN software. z-stack images were focus stacked using Picolay (www.picolay.de). Image analysis was done in ImageJ and Fiji (11, 12), and stitching of multi-images using Microsoft ICE and movement analysis was done with the ImageJ plug-in MTrackJ (13). Measurements included distance covered in one plane over time (speed), time between movement direction reversals, rotation, loop formation, and behavior over time scales from seconds to days.

Movement speed was recorded only if movement was continuous for 30 s without reversals, sudden twitching, or jerking movement caused by interaction with other cable bacteria. Both advancing loops and tips of cable bacteria were used for speed measurements. To preserve a level of randomized sampling in the measurements, the cable bacteria recorded and measured were picked by moving a small random distance clockwise around the clump of mud on a slide. Time-lapse micrographs were recorded for 3 min, but only visibly moving cables were used. To investigate the variability of speed, single cable bacteria were followed for 1 h in a type A slide while movement speed and reversals were recorded.

To test for correlations between cable bacterium diameter, speed, and the day of the incubation, Pearson's correlation coefficient was calculated for the measured cables (14). The measurements were permuted 100,000 times, from which the null distribution for the correlation coefficient was calculated. The *P* value of the observed correlations was obtained from the null distributions.

FISH identification of cable bacteria. To ascertain that the observed motile filamentous bacteria were cable bacteria, FISH identification with a probe specific for filamentous *Desulfobulbaceae* was performed on six type B slides. The slide chambers were filled with sediment and left in a high-humidity box at 20°C for 2 days. Cover glasses with attached bacteria were removed and dried out at 15°C, dehydrated by gently flooding the cover glass with a graded ethanol series (50, 75, and 96% ethanol for 3 min each), and then dried at 46°C for a few minutes. FISH using probes DSB706 (15), targeting most *Desulfobulbaceae* and *Thermodesulforhabdus*, and EUB338 (16), labeled with Cy3 and fluorescein, respectively, was performed according to previously published protocols (17), with the exception that all washing steps were done by gently flooding the cover glasses to prevent removal of attached bacteria.

RESULTS AND DISCUSSION

Cable bacteria show gliding motility. Within a few minutes of preparing a slide, filamentous bacteria moved out from the sediment, over the open surface of the microscope slide and cover glass, and toward the openings in the slide (see Video S1 in the supplemental material). No discernible differences in motility or behavior were observed between the different slide types. FISH preparations confirmed that the long motile filaments observed belonged to the *Desulfobulbaceae* family (Fig. 1A).

Cable bacteria were observed to move only when part of the filament was in contact with a surface, generally following the long axis of the filament, with no evidence of flagella or other visible means of locomotion, and thus fit the definition of gliding motility (18–20). This is the first report of gliding motility in the *Desulfobulbaceae* family, where only motility by a single polar flagellum has been known so far (21). The closest relative with filamentous morphology and gliding motility is *Desulfonema* in the family *Desulfobacteraceae* (22).

The gliding was smooth, but cable bacterial sections reversed movement direction at times, and sometimes there was a sudden movement when part of the filament appeared to lose attachment to the surface. Not all cables were moving at all times. In a randomly picked subgroup of cable bacteria ($n = 148$), 22% of observed cables were immotile, 35% were gliding tip first, and 43% were gliding as loops (described below).

Speed and reversal frequency vary. The observed cable bacteria moved with a mean speed ± standard deviation (SD) of 0.5 ± 0.3 μm s^{-1} and a maximum speed of 2.2 μm s^{-1} when moving smoothly without reversals (see Fig. S2 in the supplemental material). This was remarkably slower than other large, gliding filamentous bacteria moving at 6.0 μm s^{-1} for temperate *Beggiatoa* species (23), and 4.0 μm s^{-1} for *Desulfonema* (22). For cable bacteria moving underneath a photosynthetic mat, the estimated speed is only 0.13 to 0.23 μm s^{-1} (6). This, however, represents movement over longer time and distances, where reversals, snaring by other cable bacteria, obstruction by sediment particles, and poor orientation and coordination within a long filament may limit the overall progression. The observed standard deviation of the speed was 60% of the mean, which is 5 to 6 times higher relative variability in speed than in different *Beggiatoa* species gliding steadily at 5.6 ± 0.6, 6.0 ± 0.6, and 1.6 ± 0.2 μm s^{-1} (23).

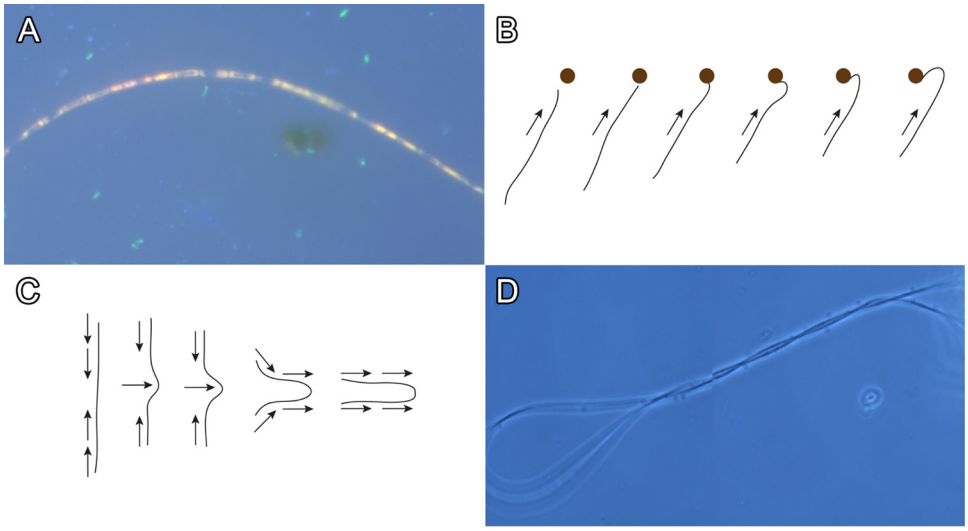

FIG 1 (A) FISH identification of cable bacteria as *Desulfobulbaceae* by probes DSB706-CY3 (red) and EUB338-fluorescein (green), resulting in a yellowish color. (B and C) Schematic representation of loop formations. In panel B, a filament encounters an obstacle, bends immediately behind the collision, and continues as a loop, and in panel C, two parts of the filament are moving in opposite directions, which causes the middle to bend out and move perpendicular to the original direction of movement. Arrows indicate direction of movement. (D) Left-handed twisted loop structures presumably formed by the rotational force present in the movement of cable bacteria.

Photokinetic cyanobacteria move at different speeds controlled by light conditions (24).

The diameters of cable bacteria varied from 0.4 to 2.2 μm, and there was no correlation between diameter and speed (Fig. 2A). The time series also revealed no significant change in the average speed during the 27 days of incubation (Fig. 2B), where the average diameter of the cables increased by about 50% (Fig. 2C). The weak correlation between diameter and speed of cable bacteria or speed and duration of incubation is similar to that found in *Beggiatoa*, where a temperature-controlled study was also unable to show a clear correlation between diameter and speed (23).

Recording the speed and direction of individual cable bacteria for 1 h showed that the time between reversals varied from 30 to 450 s, with a mean ± SD of 155 ± 108 s (see Fig. S3 in the supplemental material), giving an average uninterrupted gliding distance of 74 μm. Almost all variation in gliding speed could be attributed to variation in the speed of individual cable bacteria, rather than variation between different cable bacteria (see Fig. S2 in the supplemental material). The remaining variation may be due to the samples containing multiple strains of cable bacteria. The variation patterns, together with the weak correlation found between speed, diameter, and incubation duration in the time series data, suggested that the variability of speed is intrinsic to the way cable bacteria glide and is not controlled by any of the parameters measured in this study.

Cable bacteria frequently move as loops. More often than gliding with one tip first, cable bacteria glided with a loop first. Such loop type movement was initiated in two ways (Fig. 1B and C): when a cable bacterium gliding tip first encountered an obstacle, the tip could remain stuck on the obstacle, and the continuously moving filament created an extending loop. Alternatively, different parts of a filament were gliding in opposite directions toward each other, forming a bump that could result in a loop perpendicular to the original direction of gliding. Sometimes even very short cable bacteria of 20 to 50 μm could be seen gliding sideways as loops rather than as straight filaments (see Video S2 in the supplemental material). Once a loop had formed, gliding as a loop continued for long periods of time, and the filament typically formed two long parallel arms. Occasionally, cable bacteria would instead wind around themselves, forming twisted loops (Fig. 1D),

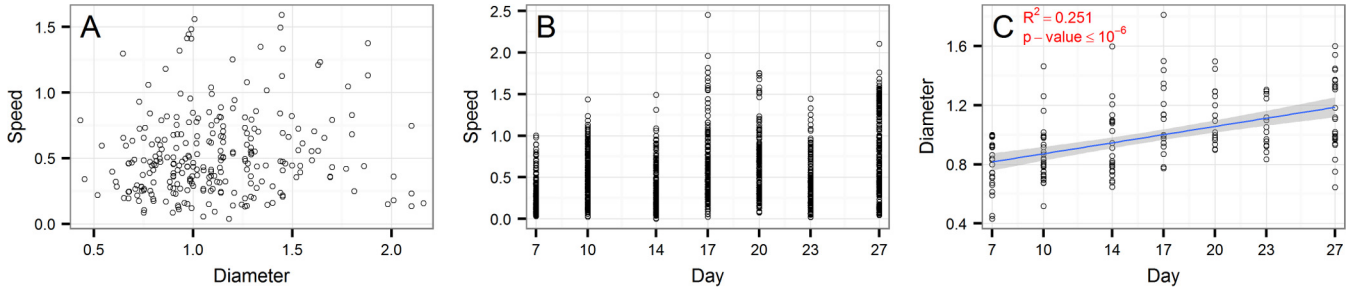

FIG 2 Correlation analysis of incubation duration, size, and speed of cable bacteria. (A) Speed and diameter of cables ($R^2 = 0.014$, $P = 0.03$, $n = 261$), (B) speed of cables and days of incubation ($R^2 = 0.115$, $P \leq 10^{-6}$, $n = 1{,}384$), and (C) cable diameter and days of incubation ($R^2 = 0.251$, $P \leq 10^{-6}$, $n = 150$). The blue line and gray area denote the best fit linear regression line together with the 95% confidence interval. The regression line for the correlation with the most support (C) is shown.

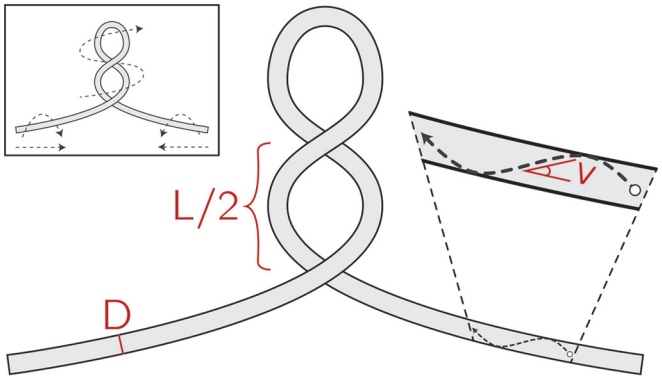

FIG 3 Schematic representation of the formation of twisted loops (not to scale). The left inset shows the directional (straight arrows) and rotational (curved arrows) forces in a cable bacterium as a twisted loop is formed. The right inset shows a closeup of the trajectory of a single point on the surface of a cable bacterium as it moves and rotates. The major terms (*D*, *L*, and *V*) for calculating the rotation angle are marked in red.

thus demonstrating rotational gliding as described for many other filamentous bacteria (18, 25). Twisting requires sufficient open space around for the rotation of the loop, and the loop then makes one complete twist for every complete rotation of the two arms. A rotational movement of a filament is typified by the rotation angle, *V*, which is the deviation from the filament direction that the path of a point on the surface takes (Fig. 3). Knowing the length of a complete winding (*L*), and the circumference of the filament ($\pi \times D$), it was therefore possible to calculate $V = \text{arcTan}\ (\pi \times D/L)$ (Fig. 3). In Fig. 1D, D/L is 1/30, and the angle is therefore 6°. For 13 such twisted loops with various filament diameters, the average ± SD rotation angle was 9 ± 2.4°. Loops with irregular twists, erratic movements, or other signs of obstructions or tensions were excluded from the survey. The rotation was preferentially left-handed, as 26 out of 27 observed twisted loops were wound to the left, and smooth unwinding of twisted loops was observed when the filament reversed its directions of movement (see Video S3 in the supplemental material). Helically arranged ridges on the surface of filamentous cyanobacteria have been found to match their filament rotation, thus serving as guides for the gliding motility (16). Reinspection of our collection of scanning electron microscopy images of straight cable bacterial segments ($n = 19$) (e.g., see Fig. 5 in the article by Pfeffer et al. [1]) showed that if their ridges with the periplasmic strings inside were helical at all, the angle was below 2°, suggesting that other structures must control rotation in cable bacteria. The adaptive importance of rotational movement is not obvious, although it possibly helps the cable bacteria to move in a more straight direction through the sediment in their natural environment.

Chemotaxis and ecological implications. The sediment cable bacteria inhabit holds many motile microaerophilic bacteria (26), and when type A or B slides were made, these bacteria formed a clearly visible veil marking the oxic-anoxic interface. Using this demarcation to track the cable bacterial movement relative to oxygen, we showed that the filaments stayed in touch with the receding oxygen front (Fig. 4; see Video S4 in the supplemental material) and stopped moving when the oxygen front stabilized its position. On type B and C slides, cable bacteria emerged from the sediment chamber and moved toward the oxygen until the leading filament part was observed to cease forward movement when reaching the microaerophilic veil. The rest of the filament continued to glide forward, causing a pileup of cable bacteria at the oxic-anoxic interface and into the oxic zone (see Video S5 in the supplemental material). The remaining, anoxic part of the filament was pulled tight, creating a straight line to the sediment (Fig. 5).

Motility is needed for cable bacteria to follow the receding sulfide front and stay connected with the oxygen while the gap between oxygen and sulfide is widening as a consequence of cable bacterial metabolism and growth. Should a cable bacterium lose contact with the separating sulfide or oxygen fronts, motility would allow it to reconnect. Cable bacteria were observed to stop gliding when in contact with oxygen and to glide when there was little or no oxygen available. This behavior is highly suggestive of oxygen chemotaxis and agrees with previous observations of cable bacterial activity in photosynthetic mats (10). Gliding motility and oxygen chemotaxis are common among other filamentous sulfide-oxidizing bacteria to effectively position them in gradient environments (25, 27, 28). The large filamentous *Beggiatoaceae* are also able to use deep sulfide sources by commuting up and

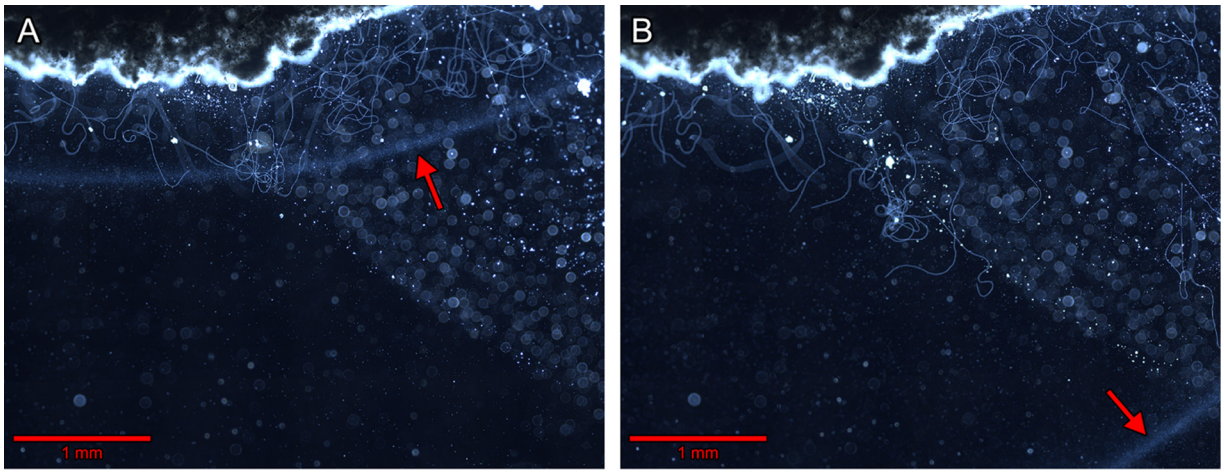

FIG 4 Cable bacteria following oxic-anoxic interphase. Red arrows indicate positions of crescent-shaped anoxic interphase. Cable bacteria are seen moving from the sediment near the top of the images downwards to where oxygen is diffusing in. (A) Initial position. (B) Position after 5 h.

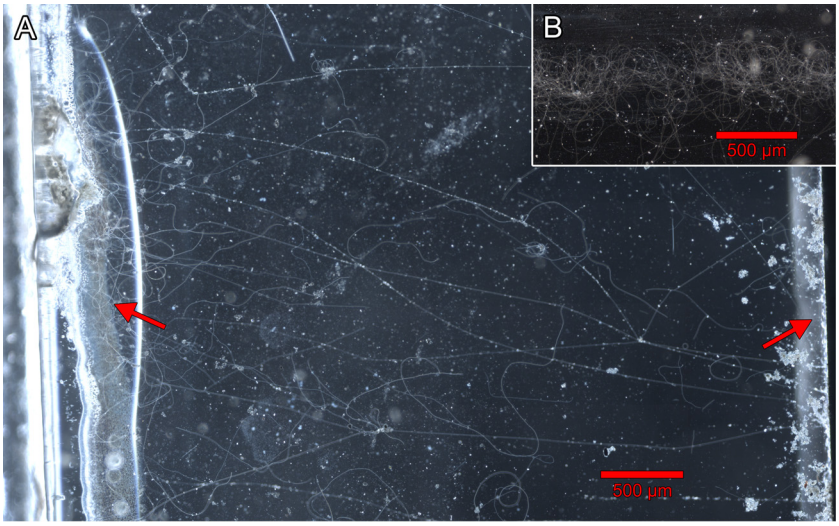

FIG 5 Positioning of cable bacteria between the oxygen-sulfide gradient on type B slides. (A) Multi-image focus-stacked z-stack, where cables have emerged from sulfidic sediment (right), moved over the glass surface, and formed a stable front of curled-up cables near the edge of the slide (left), with the rest of the cable pulled tight down to the sediment. (B) A different view of a cable pileup on a different slide.

down in the gap between gradients, using stored nitrate as a portable electron acceptor. However, due to their ability to transport electrons, cable bacteria do not need to move once they are bridging the gap between oxygen and sulfide. They therefore have less need for movement, which explains why they can afford to move much slower than other filamentous bacteria in the same environment or even stop moving. It is tempting to imagine connections forming between individual cable bacterium filaments, but despite many hours of observation, such connections have not been seen. The cable bacteria are long enough to span the whole gap individually. How they solve the problem of coordinating their movement in order to span the gap between oxygen and sulfide remains to be shown. Cable bacteria greatly influence sediment habitats (10, 29), and insight into their motility and behavior helps explain previous experimental observations and sheds light on cable bacterial function in the environment, increasing our understanding of the cable bacterium's ecological role.

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